The shield-backed bug, *Pachycoris stallii*: Description of immature stages, effect of maternal care on nymphs, and notes on life history

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Abstract

The life history of the shield-backed bug, *Pachycoris stallii* Uhler (Heteroptera: Scutelleridae), immatures was studied on its host plant, *Croton californicus* Muell.-Arg. (Euphorbiaceae), in Baja California Sur, México. Immature stages are described and illustrated. *Pachycoris stallii* is bi- or multivoltine and occurs in xeric areas with sandy soil where it is rarely encountered away from *C. californicus*. Nymphs and adults feed on seeds within *C. californicus* fruit. Bugs oviposit on the underside of leaves, and females guard their eggs and first-instar nymphs from natural enemies. Embryonic orientation of prolarvae is nonrandom; each embryo is oriented with its venter directed toward the ground. This orientation may facilitate aggregation of first instars. The longitudinal axes of eggs are always oriented upward at about a 16° angle of deviation from a line perpendicular to the leaf surface. This is the first recorded observation of this phenomenon in Pentatomoidea. Experimental removal of females guarding first instars results in 100% loss of nymphs, and this is attributed to disruption of the aggregative behavior of nymphs. Maternal guarding appears to be a net benefit to *P. stallii*, despite possible costs to the brooding female.

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Introduction

The Family Scutelleridae, or shield-backed bugs, occurs worldwide and is represented by about 80 genera and 450 species in four subfamilies (Lattin, 1964; Schuh et al., 1995). Scutellerids are members of the Pentatomoidea, and all are phytophagous. Perhaps because they are infrequently observed or collected in large numbers, little is known about scutellerids (Yonke, 1991; Schuh et al., 1995), although some are pests of wheat, cotton, and other crops (Cardona et al., 1983; Wilson et al., 1983; Grimm, 1999; Parker et al., 2002).

The genus *Pachycoris* Burmeister 1835, placed in the subfamily Pachycorinae, is distributed mainly in the New World. *Pachycoris stallii* Uhler was described in 1863; although its distribution is not well-demarcated, it is known mostly from subtropical regions of México. Like several of its congeners (Hussey, 1934; Wolcott, 1951; Grimm et al., 1998; Peredo, 2002), *P. stallii* is host-specific on a Euphorbiaceae, and exhibits aposematic coloration and subsocial behavior. Females oviposit on leaves and guard egg masses and first-instar nymphs from natural enemies (Williams et al., 2001). Wilson (1979) postulated that exceptional environmental challenges (e.g., intense pressure from natural enemies) might select for evolution of subsocial behavior in insects. Brooding *P. stallii* females apparently do not feed and therefore may be subjected to costs associated with guarding offspring, including shortened lifespan due to starvation, and increased vulnerability to natural enemies. Williams et al. (2001) reported that the chemical defense system of *P. stallii* is based on short-chain carbonyl compounds, as appears to be the norm for Heteroptera (Aldrich, 1995).

The population of *P. stallii* that we studied was discovered by one of us (LW) in Baja California Sur, México. At this site *P. stallii* is apparently highly host specific to *Croton californicus* Muell.-Arg. (Euphorbiaceae) as it was rarely encountered on other plants. *Croton californicus* is a perennial shrub that occurs in the southwestern United States and northwestern México (Shreve et al., 1964; Wiggins, 1980). In Baja California this shrub occupies sandy areas near beaches and drainages where annual precipitation and temperatures average 260 mm and 26° C, respectively (Johnson, 1977). The plant is drought-deciduous and at the study site grows as an erect, sparse shrub up to about 1 m in height. Leaves measure several centimeters in length, are gray-green, lanceolate or elliptical, and hang vertically. *Croton californicus* flowers throughout the year at the study site, producing inconspicuous male and female flowers borne on terminal racemes. Fruit are dehiscent tri-lobed capsules (ca. 5 mm diam). Phytochemical investigations have shown that leaves, stems, and fruit produce numerous toxic compounds, including terpenoids and phorbol esters (Wilson et al., 1976; Luzbetak et al., 1979; Chavez et al., 1982; Williams et al., 2001). Most herbivores, both vertebrate and invertebrate, generally avoid this chemically well-defended plant.

The purpose of this study is to describe the immature stages of *P. stallii* and present life history information on its field biology, including an experimental field study of maternal guarding of nymphs.

Materials and Methods

Field observations and collections of *P. stallii* eggs and nymphs were made on its host plant, *C. californicus*, in Baja California Sur, México (Fig. 1). The field site was visited at irregular intervals throughout the calendar year from 1988 to 1997. Some field-collected egg masses were placed in 9 dram ventilated plastic vials (Thornton Plastics, http://thorntonplastics.com) and maintained alive at about 27° C to allow the observation of color change and embryonic orientation during development.

Figure 1. Field site in Baja California Sur, México, with *C. californicus* plant in foreground.

A study was conducted to determine the effect of maternal guarding on survival of first-instar

nymphs, and to provide insight on the tradeoffs inherent in subsocial behavior. *Croton californicus* plants harboring newly emerged (≤1 day old) first-instar nymphs were chosen in a 600 x 100 m study area. The duration of the study (6 days, 27 July-1 August 1994) approximated the developmental period of first-instar nymphs during the summer. Minimum and maximum temperatures during the study ranged from 26 to 44° C (shaded temperatures 2 m above the soil; Schultheis Quick Reading Thermometer, http://www.millerweber.com). In total, 15 groups of guarded nymphs were chosen for study; five control groups and ten treatment groups. In each treatment group the adult female bug was carefully removed from the leaf and placed on another plant several meters away. Previous observations confirmed that female bugs did not return to their offspring after being displaced in this manner. Care was taken to minimize disturbance to the nymphs during this procedure. In control groups adult females were not removed. The nymphs in each of the 15 groups were then counted (day = 0); on each day thereafter (day = 1 to 5) the entire plant was searched and all unguarded first instar nymphs were counted. We assumed that these nymphs represented those included in the study. The effect of female brooding on survival of first instars was assessed by comparison of the appropriate confidence intervals (binomial distribution was used for control, normal distribution was used for treatment) on each day of the study.

While conducting fieldwork we noticed that when nymphs were disturbed they sometimes dropped from plants and hid in the leaf litter where they were probably exposed to greater risk from natural enemies as well as high surface temperatures. Therefore, we tested the ability of nymphs to survive if they fell to the sand or attempted to disperse to different plants during the summer (July). At mid-day several leaves with second or third instar nymphs were placed on the sand in direct sunlight and their behavior was recorded. A Schultheis Quick Reading Thermometer was used to measure substrate surface temperatures (direct sunlight = 54° C, in shade = 42° C).

Field-collected specimens to be used for descriptions were killed and preserved in 70% ethanol. Descriptions and terminology follow those of Decoursey and Esselbaugh (1962), Miller (1971), and Javahery (1994). At least ten specimens of each nymphal instar were measured using an ocular micrometer on a Wild M-stereomicroscope. Length of nymphs was measured from tip of clypeus to tip of abdomen, and width was measured at the widest point of the body. The fifth instar is described in detail and only major differences that are present in previous instars are described. All measurements of dimensions are given in millimeters (mean ± SD and range). Drawings of nymphs were made with a drawing tube on a Wild M-stereomicroscope.

Sample sizes varied for eggs and are given in the description. However, measurements of individual eggs were made from at least 66 individuals randomly chosen from 39 egg masses. The degree of deviation of eggs from being perpendicular to leaf surface was estimated by observing the lateral aspect of each egg mass under a dissecting scope. A protractor was positioned under the egg mass and the degree of deviation from perpendicular was recorded from the grid on the protractor. Specimens to be examined by scanning electron microscopy were dehydrated in a graded ethanol series, mounted on aluminum stubs with silver paint, and sputter-coated with gold-palladium alloy prior to examination with a JEOL T-100 scanning electron microscope.

Voucher specimens of *P. stallii* are deposited in the Museo de Arthrópodos de Baja California (CODEN: CICESE), Centro de Investigación Cientifica y de Educación Superior de Ensenada, Ensenada, Baja California, México, and in the Museo Departmento Científico de Entomología (CODEN: MLP), Facultad de Ciencias Naturales, Universidad Nacional de La Plata, La Plata, Argentina.

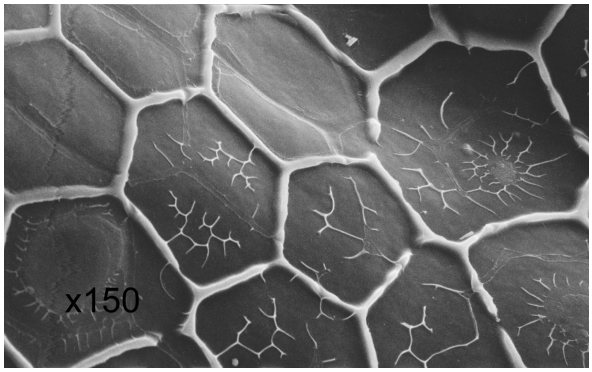
Results and Discussion

Eggs

Description. Eggs cylindrical with convex ends. Length, 1.46 ± 0.13 (1.20-1.69, n = 101); width, 0.87±0.06 (0.71-1.02, n=101). Chorion with hexagonal reticulations surrounding smaller irregular sculpturing (Fig. 2). Cephalic pole with a ring of unevenly spaced micropylar processes, 19 ± 2.08 (14-23, n = 66). Pseudoperculum circular, sometimes askew, ovate; egg burster dark brown, subtriangular, T-shaped. Chorion relatively thin, weak, and pliable, similar to that of the pentatomid *Euschistus servus* (Say). Egg masses consisted of 53.8 ± 8.86 (33-74, n =40) eggs laid in roughly hexagonal groups. The average number of rows per egg mass was 8.47 ± 0.97 (6-11, n = 30). Egg

masses averaged 6.80 ± 0.63 (5.43-8.23, n = 39) in length and 5.95 ± 0.55 (4.75-7.20, n = 39) in width.

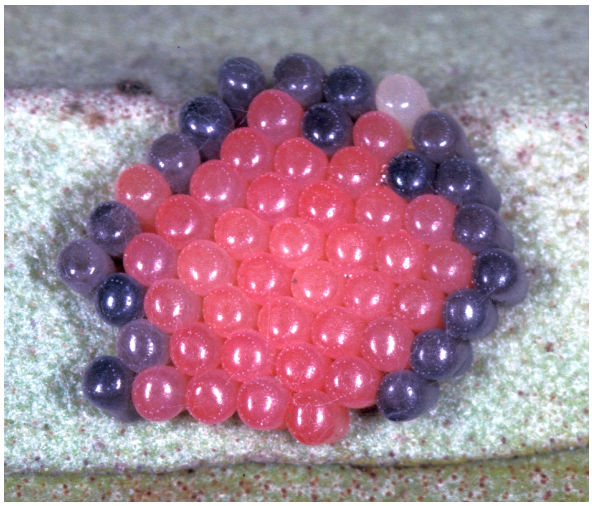
Figure 2. Chorionic reticulations of *P. stallii* egg.



Leaves with egg masses averaged 35.0 ± 7.2 in length, and 13.0 ± 4.2 (n = 35) in width. The position of egg masses on leaves corresponded to the approximate center of the leaf (92% of maximum width, 44% of maximum length measured from leaf base). Egg masses usually overlapped the midvein, but occasionally were positioned entirely between the leaf margin and midvein. The longitudinal axes of eggs were not perpendicular to the leaf surface, but instead were always oriented toward the leaf base, (i.e., upward) at an angle. This angle of deviation from a line perpendicular to the leaf surface was 15.9° ± 12.4 (5-45, n = 125). To our knowledge, this is the first recorded observation of this phenomenon in Pentatomoidea. Its function, if any, is unknown. Dimensions of egg masses were considerably less than those of adult females (egg masses: 6.80 x 5.95 mm; adult females: 11.73 x 7.83 mm), thus egg masses were completely covered by the brooding females. The longitudinal axis of an egg mass was usually parallel to that of the leaf. Eberhard (1975) also reported this egg mass orientation for the pentatomid *Antiteuchus tripterus limbativentris* Ruckes and suggested that it might be due to the consistent position of the defending bug in relation to the orientation of the egg mass, as influenced by selection pressure of parasitic wasps.

Immediately after oviposition, eggs were cream-colored. As embryonic development proceeded, the embryos acquired a concolorous pigmentation of pale pink except for a cream-colored band extending from the caudal to cephalic region. With further development, the eggs became pinkish orange, noticeable first in the eyes, clypeus, pronotum, and appendages. Finally, about 4 days after oviposition the embryos transformed to salmon, then darkened to red prior to eclosion. Hatching was observed on two occasions, both in the morning (28 July 1994, 0741-0751 h, 34° C, two separate egg masses). When embryonic cuticles were recovered (n = 83), they were matted together either on the portion of the egg mass nearest the leaf tip, or occasionally on the leaf just distal to this portion of the egg mass. Some of the eggs failed to develop (≤10%), and these undeveloped eggs remained creamy yellow. Color changes observed during development of *P. stallii* eggs were similar to those reported for other *Pachycoris* species (Hussey, 1934; Grimm et al., 1998; Peredo, 2002). Most *P. stallii* egg masses were parasitized by a wasp, *Telenomus pachycoris* (Costa Lima) (Hymenoptera: Scelionidae); parasitism rates averaged about 47% (Fig. 3). Parasitized eggs turned from gray to black as the parasitoids developed. Antagonism by ants, *Dorymyrmex bicolor* Wheeler (Hymenoptera: Formicidae), sometimes caused brooding *P. stallii* females to abandon their egg masses, after which the ants devoured the eggs (Fig. 4).

Figure 3. Egg mass of *P. stallii* on *C. californicus* leaf. Unparasitized, apparently healthy eggs are red; eggs parasitized by *T. pachycoris* are black, and the undeveloped egg is creamy yellow.



Lockwood and Story (1986a) postulated that nonrandom embryonic orientation, i.e., dorsoventral polarity, of prolarvae is an adaptive function that reduces mortality of first instars. We

assessed the embryonic orientation for *P. stallii* prolarvae within egg masses that were not parasitized by *T. pachycoris*. These unparasitized egg masses were similar to those described previously, consisting of 55.4 ± 11.06 (34-73, n = 14) eggs. Embryonic orientation in these egg masses was not related to position of egg within the mass. Instead, each embryo was oriented with its venter directed down (i.e., toward the ground) regardless of the location of the egg within the mass. Other studies also reported uniform embryonic orientation in scutellerids. Javahery (1994) reported that eggs of *Eurygaster alternata* (Say), *E. integriceps* Puton, and *E. maura* (L.) were oriented in one direction, as did Reid and Barton (1989) for *Chelysomidea guttata* (Herrich-Schaeffer). However, neither study indicated the direction of the embryos. Eberhard (1975) found that embryos of the pentatomid *A. t. limbativentris* were all oriented in the same direction in each egg mass, although neither the direction of embryos in an egg mass nor differences in embryonic orientation between egg masses were reported. However, embryonic orientation of other pentatomid species was dependent on egg location within the mass, as influenced by form of egg mass, number of eggs, and number of rows in an egg mass, and could be described as a 'center orientation' for emerging nymphs (Lockwood et al., 1986a; Javahery, 1994). Lockwood and Story (1986a) demonstrated that embryonic orientation in *Nezara viridula* (L.) varied with egg position within the mass, was extrinsically mediated, and facilitated formation of first-instar aggregations. This 'center orientation' of embryos enhanced survival and development of *N. viridula* (Lockwood et al., 1986b), and may serve a similar function in other pentatomoids. Although the embryonic orientation of *P. stallii* differed from that described for most pentatomoids, it may nevertheless provide an adaptive function. The uniform downward embryonic orientation of *P. stallii* may facilitate formation of first-instar aggregations at a relatively safe location on the leaf (i.e., between the egg mass and the distal tip of the leaf). This would position the brooding female bug between the nymphs and the only route by which crawling natural enemies could gain access to the leaf. Thus, the mother would be in a position to defend her offspring.

Figure 4. *Dorymyrmex bicolor* eating *P. stallii* eggs after egg mass was abandoned by brooding female.

Nymphs

Descriptions

First Instar (Fig. 5a). Color as for fifth instar, without metallic green. General color red. Legs pale brown, tinged with red. Eyes red. Total length, 2.57 ± 0.05 (2.50-2.60). Length of head, 0.62 ± 0.02 (0.60-0.63); width of head, 0.88 ± 0.01 (0.87-0.90). Width of eye, 0.12 ± 0.01 (0.12-0.13); interocular space, 0.64 ± 0.01 (0.63-0.65). Rostral length, 1.17 ± 0.07 (1.08-1.25). Antennal length, 1.11 ± 0.05 (1.03-1.15); ratio of segment lengths about 1:1.78:1.64:3.43. Length of pronotum, 0.25 ± 0.01 (0.24-0.25); width of pronotum, 1.09 ± 0.04 (1.03-1.13). Abdominal length, 1.41 ± 0.04 (1.37-1.47); abdominal width 1.66 ± 0.06 (1.60-1.73).

Second Instar (Fig. 5b). Color as for fifth instar, without metallic green. Legs dark brown. Abdomen red. Eyes red. Total length, 3.27 ± 0.09 (3.20-3.40). Length of head, 0.78 ± 0.02 (0.75-0.80); width of head, 1.19 ± 0.03 (1.15-1.22). Width of eye, 0.19 ± 0.01 (0.18-0.20); interocular space, 0.81 ± 0.02 (0.78-0.83). Rostral length, 2.14 ± 0.1 (2.00-2.22); ratio of segment lengths about 1:2:1.34:1.29. Antennal length, 1.75 ± 0.05 (1.70-1.82); ratio of segment lengths about 1:1.65:1.5:2.58. Length of pronotum, 0.38 ± 0.01 (0.37-0.40); width of pronotum, 1.50 ± 0.06 (1.42-1.57). Abdominal length, 1.65 ± 0.08 (1.57-1.75); abdominal width, 2.10 ± 0.12 (2.00-2.27).

Third Instar (Fig. 5c). Color as for fifth instar, without metallic green. Eyes dark red. Abdomen red. Total length, 4.29 ± 0.1 (4.18-4.43). Length of head, 0.94 ± 0.13 (0.75-1.17); width of head, 1.69 ±

0.04 (1.63-1.75). Width of eye, 0.29 ± 0.02 (0.27-0.32); interocular space, 1.11 ± 0.04 (1.05-1.17). Rostral length, 2.93 ± 0.07 (2.89-3.05); ratio of segment lengths about 1:2.11:1.21:1.31. Antennal length, 2.65 ± 0.04 (2.64-2.75); ratio of segment lengths about 1:2.15:2.03:2.85. Length of pronotum, 0.62 ± 0.03 (0.58-0.65); width of pronotum, 2.28 ± 0.16 (2.08-2.51). Abdominal length, 2.34±0.37 (1.98-2.81); abdominal width, 2.87 ± 0.36 (2.48-3.35). Stridulitrum on venter of abdomen consisting of a series of coarse fingerprint-like elongate ridges on sternites 5, 6, and anterior portion of 7, less pronounced than in fourth instar.

Fourth Instar (Fig. 5d). Eyes dark red. Total length, 5.23 ± 0.21 (4.94-5.38). Length of head, 0.98 ± 0.17 (0.83-1.24); width of head, 2.27 ± 0.03 (2.23-2.30). Width of eye, 0.39 ± 0.01 (0.30-0.40); interocular space, 1.48 ± 0.02 (1.45-1.50). Rostral length, 3.32 ± 0.02 (3.30-3.35); ratio of segment lengths about 1:2:1.19:1.25. Antennal length, 3.64 ± 0.04 (3.60-3.69); ratio of segment lengths about 1:1.92:1.86:2.37. Length of pronotum, 0.97 ± 0.05 (0.90-1.00); width of pronotum, 3.82 ± 0.08 (3.74-3.94). Wing pad length, 1.22 ± 0.06 (1.15-1.30). Abdominal length, 2.76 ± 0.21 (2.53-3.04); abdominal width, 4.28 ± 0.17 (4.05-4.43). Stridulitrum on venter of abdomen consisting of a series of coarse fingerprint-like elongate ridges on sternites 5, 6, and anterior portion of 7, less pronounced than in fifth instar.

Fifth Instar (Fig. 5e). Total length, 6.77 ± 0.46 (6.33-7.41). Length of head, 1.01 ± 0.30 (0.63-1.37); width of head, 2.91 ± 0.09 (2.79-3.00). Body broadly oval; shiny, coarsely punctate. Head dark brown, almost black, with a metallic green sheen; laterally dark brown except under the eyes, brown. Bucculae pale brown. Clypeus not surpassing the jugae, with short, sparse setae. Eyes prominent, rounded from lateral view, nearly contiguous with pronotum. Eyes dark red. Width of eye, 0.56 ± 0.02 (0.53-0.58); interocular space, 1.90 ± 0.05 (1.83-1.93). Rostrum dark brown. Rostral length, 4.46 ± 0.02 (4.57-4.60); ratio of segment lengths about 1:1.79:0.96:1.2. Antennae dark brown, almost black, union between segments pale brown; short abundant setae. Antennal length, 5.31 ± 0.09 (5.20-5.40); ratio of segment lengths about 1:2.41:2.18:2.22.

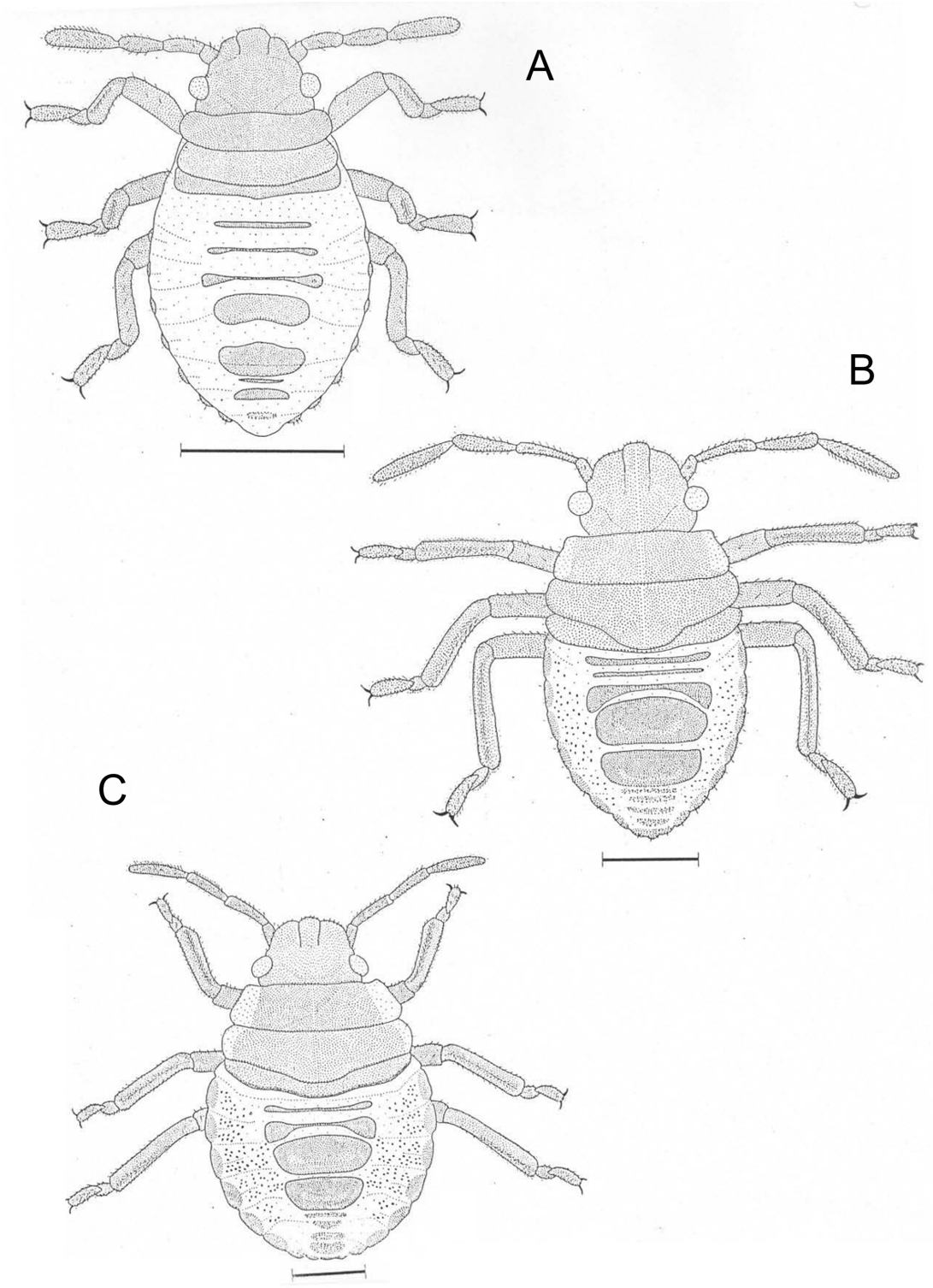
Abdominal length, 3.58 ± 0.08 (3.48-3.67); abdominal width, 5.57 ± 0.23 (5.38-5.89). Abdomen pale brown medially, laterally tinged with orange, rugose; dark brown, almost black with metallic green plates. Ventrally brown, medially pale brown, rugose; laterally tinged with orange, dark brown plates (Fig. 5f); sparsely setose. Paired ostia of dorsal abdominal scent glands located between terga 3 and 4, 4 and 5, and 5 and 6, with reticulate microsculpturing near ostiole and occlusion arm (see Williams *et al.* 2001). Using the criteria of Remold (1962), ostioles of the anterior dorsal abdominal glands of type 1 (undivided ostiole), while median and posterior ostioles intermediate between types 1 and 2 (divided ostiole). Stridulitrum on venter of abdomen consisting of a series of coarse fingerprint-like elongate ridges on sternites 5, 6, and anterior portion of 7 (Fig. 6a,b). Ventral surface of metathoracic tibia with ridges with ca. 20 small tubercules (Fig. 6c,d).

Thorax with three distinct segments. Pronotum dark brown, almost black, with metallic green sheen, except edges brown tinged with orange, flat laterally; punctate. Length of pronotum, 1.60±0.14 (1.43-1.77); width of pronotum, 5.55±0.12 (5.38-5.63). Meso- and metasternum brown. Wing pad length, 2.98±0.04 (2.93-3.03); dark brown, almost black, with metallic green sheen. Ventrally pale brown, tinged with orange. Legs dark brown, almost black; sparsely setose. Tarsi with pulvilli and parempodia as seen in Figure 6e.

Dimensions of *P. stallii* nymphs were similar to those of *P. klugii* studied in México (Peredo, 2002), although *P. stallii* had a slightly shorter antenna, rostrum, and head. Fourth- and fifth-instar *P. stallii* had smaller bodies overall (i.e., length and width) than *P. klugii* (Peredo, 2002). Dimensions of *P. klugii* nymphs studied in Nicaragua (Grimm et al., 1998) were considerably larger than *P. stallii*. As with eggs, these differences may be proportional to adult body size.

Life History and Development of Nymphs. All nymphal instars, as well as adults and eggs, were found throughout the year; thus, *P. stallii* appears to be bi- or multivoltine. After eclosion, first instars remained aggregated on or near the egg mass from which they hatched, and were guarded by the mother (Fig. 7). These nymphs were relatively inactive and were usually in contact with one another and sometimes the mother. Aggregation of first instars with the attending mother is consistent with other species of *Pachycoris* (Hussey, 1934;

Figure 5. Nymphal instars of *P. stallii*, general dorsal view; first instar (A), second instar (B), third instar (C), fourth instar (D), fifth instar (E), ventral plates of abdomen on fifth instar (F), scale bar = 1 mm.



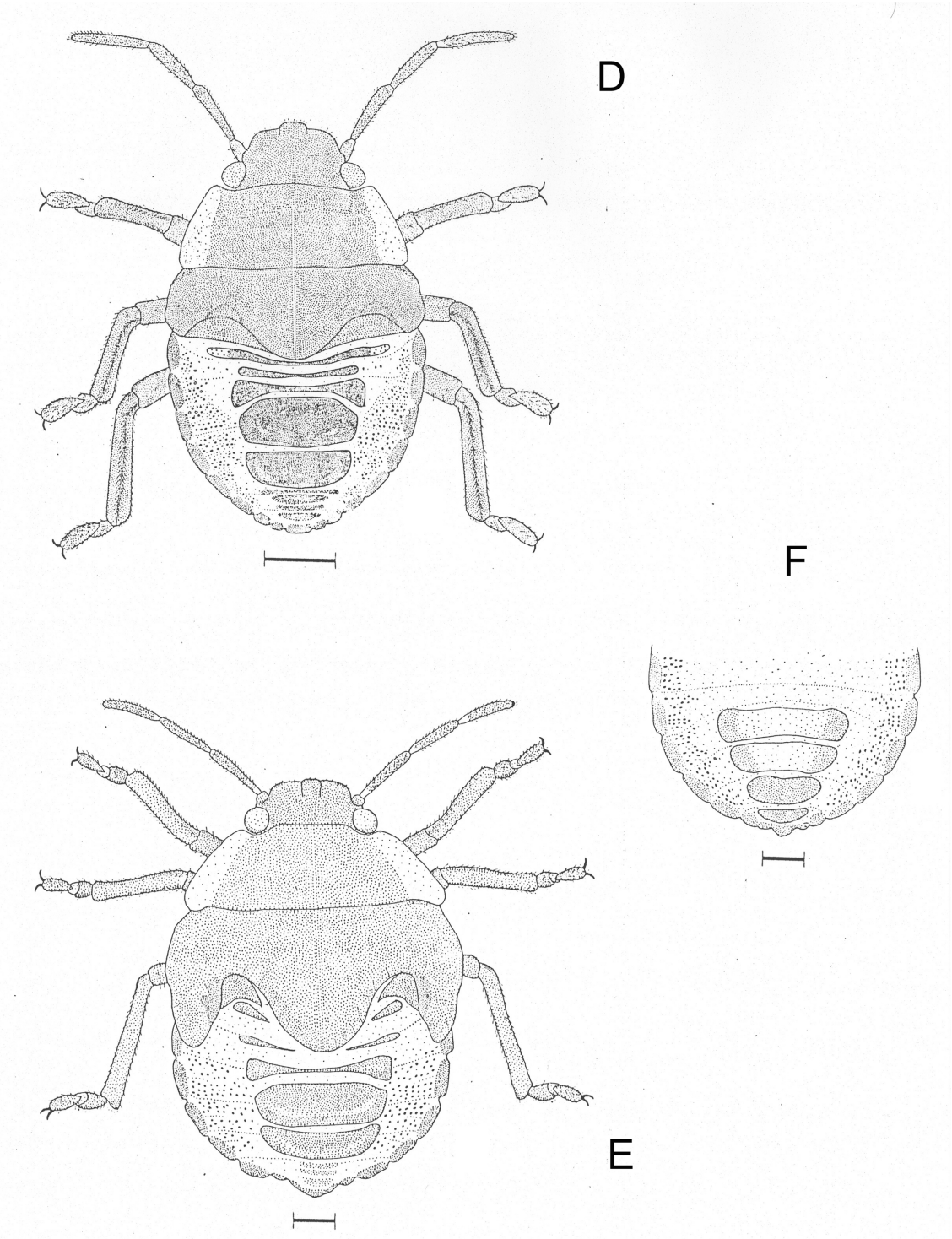
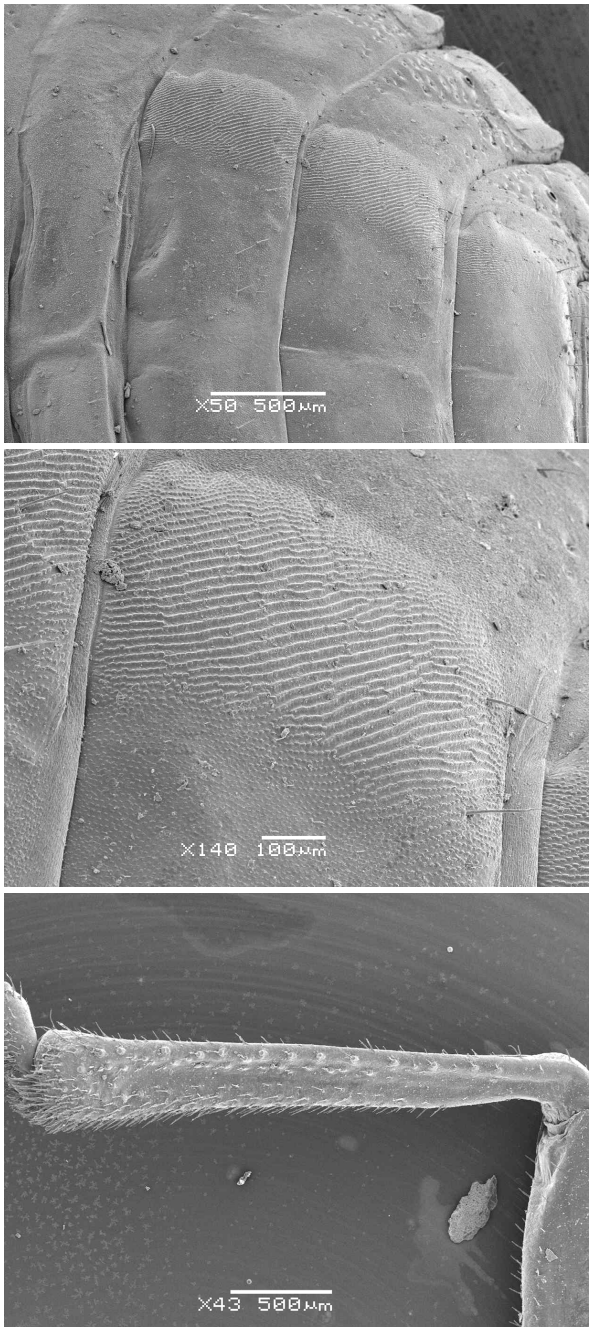
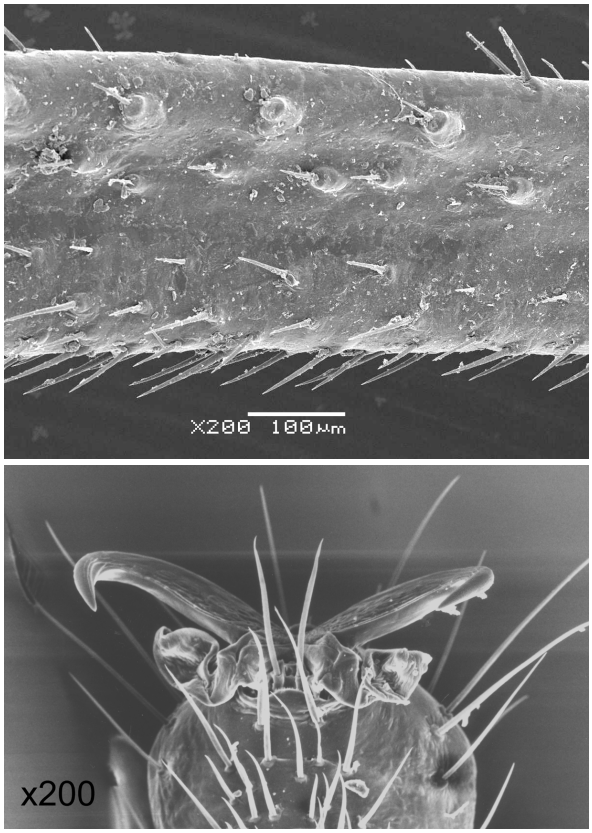


Figure 6. SEMs of stridulitrum on venter of abdomen (A & B), ventral surface of metathoracic tibia with ridge of protuberances (C & D), fifth instar pretarsus (E).



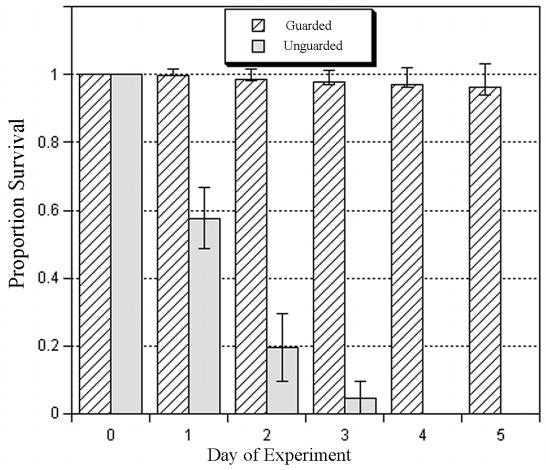


Grimm et al., 1998; Peredo, 2002). Female bugs brooding eggs were never observed feeding. First-instar *P. stallii* also appeared to abstain from feeding, as do first instars of many other Pentatomoidea (Walt et al., 1972; Eberhard, 1975; Oetting et al., 1975; Peredo, 2002).

The effect of maternal brooding behavior on survival of first-instar nymphs was evaluated by experimental removal of female bugs guarding nymphs that had just emerged. Our results indicated that brooding of first instars significantly increased their survival ($P<0.05$) (Fig. 8). Removal of guarding female bugs resulted in a rapid increase in nymphal mortality, reaching 100% after 4 days. Mortality of untreated controls was less than 4% at the end of the 6-day study. Behavior of first instars in the absence of the guarding adult was noticeably different from nymphs that were guarded. Unguarded nymphs often separated into two or three groups within a day after removal of the guarding female, and dispersed to other parts of the plant, often the apex of stems. Although predation of nymphs was not observed during the study, it is possible that disruption of nymphal aggregations

Figure 7. First instar *P. stallii* nymphs aggregated with mother on natal *C. californicus* leaf.

Figure 8. Effect of maternal brooding on survival of first instar *P. stallii* nymphs. Proportion survival (mean±SE) for guarded and unguarded nymphs. Average eggs per mass, guarded = 48.6; unguarded = 56.4. Estimation of confidence intervals in guarded nymphs (control) based on binomial distribution because mean proportion survival was close to 1, thus not normally distributed. Estimation of confidence intervals in unguarded nymphs (treatment) based on normal distribution.



predisposes nymphs to greater predation. However, Grimm and Somarriba (Grimm et al., 1998) found that first-instar *P. klugii* reared in outdoor cages that excluded most if not all predators also suffered 100% mortality when abandoned by the mother. *Antiteuchus t. limbativentris* first instars suffered substantial losses (≥40%) when guarding mothers were experimentally removed (Eberhard, 1975). Results of these studies indicate that the presence of the brooding mother plays a critical role in the aggregative behavior of nymphs and their subsequent survival. The mechanism is unknown, but it is possible that brooding *Pachycoris* females provide a cue, chemical and/or physical, that is necessary for the stability of nymphal aggregations. Our results suggest that maternal guarding behavior is a net benefit to *P. stallii*. Possible costs to the brooding female, such as starvation and increased risk from natural enemies, await further study. Eberhard (1975) also showed that the net effect of maternal guarding of first-instar *A. t. limbativentris* was positive.

Second-instar nymphs remained aggregated, but did not remain near the brooding female. We did not observe separation of these nymphs and the adult, but *P. klugii* nymphs moved away from the mother after molting to second instar (Peredo, 2002). However, Eberhard (1975) reported the reverse situation for *A. t. limbativentris* ; mothers abandoned their second-instar offspring. Aggregations of second-instar *P. stallii* were most commonly observed feeding on *C. californicus* fruit (Fig. 9a) or resting on leaves (Fig. 9b). They were much more active than first instars and readily crawled away when disturbed. Third through fifth instars were also very active, and exhibited similar feeding and resting behavior (Fig. 10) as second instars. However, aggregations of third through fifth instars consisted of progressively fewer individuals with age, so that fifth instars were usually solitary. This may be a result of cumulative nymphal mortality and/or normal decay of aggregative behavior. In contrast to what we observed, Grimm and Somarriba (Grimm et al., 1998) found that aggregations of *P. klugii* nymphs remained intact until after adult metamorphosis. Molting in *P. stallii* was observed on two occasions (28 July 1994, 0701 hours, 31° C, emergence of a fourth instar; 19 January 1997, 1353 hours, 27° C, a callow fourth instar on leaf in shade 7.5 cm above soil). On 28 December 1990, 1200-1415 hours the behavior of nymphs and adults was observed during a light/moderate rain. These conditions had no apparent effect on the behavior of *P. stallii* ; bugs were active feeding and resting as usual. During the summer months nymphs were generally observed either resting in shaded portions of the plant canopy, or if in direct sunlight, were nearly always feeding on fruit or occasionally on the stem.

Figure 9. Aggregations of second instar *P. stallii* nymphs feeding on *C. californicus* fruit (A), and resting on a leaf (B).

Figure 10. Fifth instar *P. stallii* nymph feeding on *C. californicus* fruit.

Pachycoris stallii nymphs are subject to biotic and abiotic mortality factors. Predation on *P. stallii* nymphs was rarely observed. Adult female *Zelus sulcicollis* Champion (Heteroptera: Reduviidae) were observed feeding on third-instar nymphs on two occasions (15 April 1990, 1500-1530 hours; 1 November 1995, 1515 hours in the plant canopy about 3 cm above soil surface). Ants, *Dorymyrmex bicolor*, were sometimes observed attacking nymphs on the soil beneath *C. californicus*. When leaves harboring nymphs were placed on the sand in direct sunlight the nymphs crawled to and fro on the leaf and within 5 min all had fallen or crawled off the leaf onto the sand; within 2 min they became immobilized by the heat and after an additional 2 min they died. Within 30 min they were found by *D. bicolor*. These observations indicate that typical surface temperatures during summer days are lethal to *P. stallii* nymphs that fall from plants, and thus interplant dispersal by nymphs is unlikely. However, it is possible that nymphs could survive surface temperatures during summer nights or during other seasons when temperatures are more moderate, although interplant dispersal *via* the ground might still expose them to greater risk of predation. These limits to nymphal dispersal suggest that nymphs usually mature to adulthood on their natal host plant. Clearly, much remains to be learned about the biology of *P. stallii*. Future studies will address *P. stallii* -natural enemy associations, and the effect of environmental factors on the life history of this bug.

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References

Aldrich JR. 1995. Chemical communication in the true bugs and parasitoid exploitation. In: RT Cardé, WJ Bell, editors. *Chemical Ecology of Insects* 2, 318-363. Chapman & Hall.

Cardona CF, Hariri F, El Haramein J, Rashwani A, Williams PC. 1983. Infestation of wheat by Suni bug (*Eurygaster* spp.) in Syria. *Rachis* 2: 3-5.

Chavez PI, Jolad SD, Hoffmann JJ, Cole JR. 1982. Four new 12-deoxyphorbol diesters from *Croton californicus*. *Journal of Natural Products* 45: 745-748.

Cobben RH. 1968. *Evolutionary Trends in Heteroptera. Part 1. Eggs, Architecture of the Shell, Gross Embryology and Eclosion*. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands. 459 pp.

Decoursey RM, Esselbaugh CO. 1962. Descriptions of the nymphal stages of some North American Pentatomidae (Hemiptera: Heteroptera). *Annals of the Entomological Society of America* 55: 323-341.

Eberhard WG. 1975. The ecology and behavior of a subsocial pentatomid bug and two scelionid wasps: strategy and counterstrategy in a host and its parasites. *Smithsonian Contributions to Zoology* 205: 1-39.

Esselbaugh CO. 1946. A study of the eggs of the Pentatomidae (Hemiptera). *Annals of the Entomological Society of America* 34: 667-691.

Grimm C. 1999. Evaluation of damage to physic nut (*Jatropha curcas*) by true bugs. *Entomologia Experimentalis et Applicata* 92: 127-136.

Grimm C, Somarriba A. 1998. Life cycle and rearing of the shield-backed bug *Pachycoris klugii* in Nicaragua (Heteroptera: Scutelleridae). *Entomologia Generalis* 22: 211-221.

Hussey RF. 1934. Observations on *Pachycoris torridus* (Scop.), with remarks on parental care in other Hemiptera. *Bulletin of the Brooklyn Entomological Society* 29: 133-145.

Javahery M. 1994. Development of eggs in some true bugs (Hemiptera – Heteroptera). Part I. Pentatomoidea. *The Canadian Entomologist* 126: 401-433.

Johnson AF. 1977. A survey of the strand and dune vegetation along the Pacific and southern gulf coasts of Baja California, Mexico. *Journal of Biogeography* 7: 83-99.

Lattin JD. 1964. *The Scutellerinae of America north of Mexico (Hemiptera: Heteroptera: Pentatomidae)*. Ph. D. dissertation, University of California, Berkeley. 346 pp.

Lockwood JA, Story RN. 1986a. Embryonic orientation in pentatomids: its mechanism and function in southern green stink bug (Hemiptera: Pentatomidae). *Annals of the Entomological Society of America* 79: 963-970.

Lockwood JA, Story RN. 1986b. Adaptive functions of nymphal aggregation in the southern green stink bug, *Nezara viridula* (L.). *Environmental Entomology* 15: 739-750.

Luzbetak DJ, Torrance SJ, Hoffmann JJ, Cole JR. 1979. Isolation of (-)-hardwickiic acid and 1-triacontanol from *Croton californicus*. *Journal of Natural Products* 42: 315-316.

Miller NCE. 1971. *The Biology of the Heteroptera*. Second Edition. E. W. Classey, Hampton. 206 pp.

Oetting RD, Yonke TR. 1975. Immature stages and notes on the biology of *Euthyrhynchus floridanus* (L.) (Hemiptera: Pentatomidae). *Annals of the Entomological Society of America* 68: 659-662.

Parker BL, Costa SD, Skinner M, El Bouhssini M. 2002. Sampling sunn pest (*Eurygaster integriceps* Puton) in overwintering sites in northern Syria. *Turkish Journal of Agriculture and Forestry* 26: 109-117.

Peredo LC. 2002. Description, biology, and maternal care of *Pachycoris klugii* (Heteroptera: Scutelleridae). *The Florida Entomologist* 85: 464-473.

Reid JL, Barton HE. 1989. Laboratory rearing of *Chelysomidea guttata* (Hemiptera: Scutelleridae) with descriptions of immature stages. *Annals of the Entomological Society of America* 82: 737-740.

Remold H. 1962. Über die biologische Bedeutung der Duftdrüsen bei den Landwanzen (Geocorisae). *Zeitschrift fur Vergleichende Physiologie* 45: 636-694.

Schuh RT, Slater JA. 1995. *True bugs of the world (Hemiptera: Heteroptera). Classification and natural history*. Cornell University Press, Ithaca, NY. 416 pp.

Shreve F, Wiggins IL. 1964. *Vegetation and Flora of the Sonoran Desert* (2 vols.) Stanford University Press, Stanford, California. 1740 pp.

Walt JF, McPherson JE. 1972. Laboratory rearing of *Stethaulax marmoratus* (Hemiptera: Scutelleridae). *Annals of the Entomological Society of America* 65: 1242-1243.

Walt JF, McPherson JE. 1973. Descriptions of immature stages of *Stethaulax marmorata* (Hemiptera: Scutelleridae). *Annals of the Entomological Society of America* 66: 1103-1107.

Wiggins IL. 1980. *Flora of Baja California*. Stanford University Press, Stanford, California. 1025 pp.

Williams L III, Evans PE, Bowers WS. 2001. Defensive chemistry of an aposematic bug, *Pachycoris stallii* Uhler and volatile compounds of its host plant *Croton californicus* Muell.-Arg. *Journal of Chemical Ecology* 27: 203-216.

Wilson EO. 1979. *The Insect Societies*. The Belknapp Press of Harvard, Cambridge. 548 pp.

Wilson LT, Booth DR, Morton R. 1983. The behavioural activity and vertical distribution of the cotton harlequin bug *Tectocoris diopthalmus* (Thunberg) (Heteroptera: Scutelleridae) on cotton plants in a glasshouse. *Journal of the Australian Entomological Society* 22: 311-317.

Wilson SR, Neubert LA, Huffman JC. 1976. The chemistry of the Euphorbiaceae. A new diterpene from *Croton californicus*. *Journal of the American Chemical Society* 98: 3669-3674.

Wolcott J. 1951. The insects of Puerto Rico: Hemiptera. *Journal of the Department of Agriculture University of Puerto Rico* 32: 190-191.

Yonke TR. 1991. Order Hemiptera. In: FW Stehr, editor. *Immature Insects*. Vol. 2, pp. 22-65. Kendall/Hunt Publishing, Dubuque, Iowa.